A New Take on Anthropoid Origins

The search for the ancestors of the higher primates, a group that includes humans, takes a surprising turn as old candidates fall out of favor and new ones emerge

DURHAM, NORTH CAROLINA—For almost 100 years, paleoanthropologists have been arguing about a crucial step along the evolutionary road that led to humans: Where did the first monkeys come from? In a field renowned for sharp disputes, this question has created an unusually stubborn difference of opinion, with researchers largely split into two opposing camps, each favoring a different group of primitive primates as the most likely ancestor of anthropoids—the group of higher primates that includes humans as well as monkeys and apes.

But last month, at a workshop that brought together some of the leading lights of paleoanthropology in hopes that they could at least agree on what they disagree about, the debate took a surprising new turn: Many participants concluded that anthropoids did not descend from either of the two current leading candidates. Indeed, two new candidates were nominated for that honor. Although it's too early to say whether either of these will win out, it's clear that new fossil finds of the past few years are causing many paleoanthropologists to revise dramatically their view of anthropoid origins.

Not only did some mysterious "third group" apparently give rise to the anthropoids, but the anthropoid lineage may have emerged as many as 50 million or even 60 million years ago, at least 10 million years earlier than previously thought. What's more, Africa, or possibly Asia, is the likely site of anthropoid evolution, although most of the early primate fossils have been unearthed thus far in Europe and North America. "The whole complexion of the field has changed, thanks to the rapidity of finding new material," says paleoanthropologist Susan Ford of Southern Illinois University in Carbondale.

Paleoanthropologists have had trouble pinning down the origins of anthropoids partly because ancient primates have left a muddy and incomplete trail of fossil clues. What is known is that about 55 million years ago, primates as well as other mammals began to radiate into a dazzling array of new species. At some point, one group diverged from the lower primates (or prosimians) and gave rise to the anthropoids. But no one can say with certainty what this ancestor looked like, because there's a large gap in the fossil record between primitive and advanced forms. "You put all the primates into a pile and you can always sort the anthropoids from the others," says John G. Fleagle of the State University of New York at Stony Brook. "They're so distinctive it's hard to figure out where they came from." For example, anthropoids tend to have low and rounded cusps on their teeth, as compared to the sharp relief found on the teeth of prosimians. Also, in anthropoids the two halves of the lower jaw are completely fused together, and the back of the eye is completely enclosed in a bony cup; almost all prosimians lack these characteristics.

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In between. *Tarsius*, a living primate, has been linked by some to both omomyids and anthropoids.

The lack of transitional fossil forms hasn't stopped paleoanthropologists from selecting their favorite candidates for the anthropoids' predecessors, however, and researchers have tended to choose up sides and stick to them. "It's an advocacy approach—sort of like the American legal system," says Fleagle. With that analogy in mind, Fleagle and colleagues Richard F. Kay and Elwyn L. Simons, both of Duke University, decided to bring together "in the same courtroom" at Duke a select group of 30 paleoanthropologists, representing all sides of the debate. They were to bring with them the physical evidence, which in this case means fossils or casts of ancient primates. Not that the organizers expected to change anyone's mind overnight. But the hope was to focus debate at least on which features of which fossils are cause for dispute.

For the past few decades, one major camp has argued that anthropoids are most closely related to the omomyids, an extinct group of tiny nocturnal primates that ate fruit and insects and probably gave rise to an unusual living primate called *Tarsius*. Meanwhile, a smaller—but no less stubborn—band of scientists have favored the adapids, which were larger than the omomyids, mostly diurnal, and preferred to munch on leaves and fruit. Their descendants are believed to include two related groups of primitive living primates, lemurs and lorises. Both adapids and omomyids were abundant in North America and Europe between 30 million and 50 million years ago, and relatively few of their fossils have been found in Africa and Asia.

But the more paleoanthropologists accumulated adapid and omomyid fossils from the northern continents, the more they became convinced that neither group works as an anthropoid ancestor, explained omomyid specialist Herbert Covert of the University of Colorado in Boulder. For example, in North America, paleontologists have uncovered a detailed record of an evolutionary flowering of omomyids. But trying to trace anthropoids from these creatures has become what one workshop participant called "a frustrating exercise." Instead, most of the North American lineages apparently died out. "The [fossil] animals from North America aren't ancestors [of anthropoids]. They're cousins," says Covert.

Indeed, says Fleagle, "we're finally coming to grips with the fact that you can't force anthropoids out of either of these two well-known groups." Agrees K. Christopher Beard of the Carnegie Museum of Natural History in Pittsburgh: "For the past 20 years we've been given a false choice, adapids or omomyids. I think the answer is almost certainly 'none of the above.' " At the workshop, several presenters evaluated existing evidence and concluded that in fact, adapids and omomyids—and their putative descendants, tarsiers and lemurs—may be more closely related to each other than either is to anthropoids.

This new hypothesis is a long way from universal acceptance. But it was strengthened by new fossil finds in China and Algeria, ranging in age from about 45 million to 50 million years old and presented at the workshop as possible "third group" candidates. Before these discoveries, the oldest undisputed anthropoids were fossils from the Fayum Depression in Egypt, estimated to be about 38 million years old. Not surprisingly, then, both the Chinese and Algerian fossils were star attractions at the workshop, and participants spent hours poring over microscopes studying them.

The Chinese fossils, collected at a promising new site about 50 kilometers west of

Shanghai, won the prize for most controversial. The fossils are estimated to be about 45 million years old, according to their discoverer, Qi Tao of the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing, who is working with American collaborator Beard. "I'll put my head on the chopping block," said Beard, showing slides of a fossil jaw of a primate estimated to have weighed 100 grams—roughly the size of a small chipmunk. "I believe these animals are anthropoids, and that they are very different from omomyids and adapids."

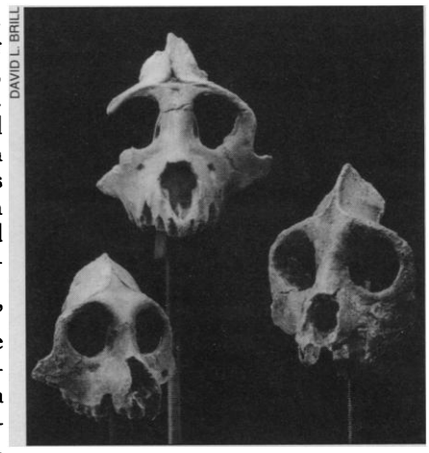
But although his colleagues were excited by the fossils, many were not convinced by what they saw. "I just wish you'd tell me what's anthropoid about this thing," said Kenneth Rose of Johns Hopkins University—Beard's former thesis adviser—as he rose from the microscope, shaking his head. Philip Gingerich of the University of Michigan was even more negative, although his was a minority opinion. "I think these things are hedgehogs, broadly speaking," he announced, after looking at casts of two jaws of Qi and Beard's putative anthropoid.

Oldest anthropoid? The Algerian fossils, discovered by Marc Godinot of the University of Montpellier and Mohamed Mahboubi of the University of Oran, Algeria, and published in part in *Nature* on 28 May, got a better reception. There was some skepticism because the material is fragmentary, consisting only of isolated teeth of what Godinot interprets as several distinct primate species. The majority of participants agreed that the teeth were primate and that at least one species, aptly named *Algeripithecus minutus* because the animal probably weighed only 150 to 300 grams, was probably on the anthropoid line. In fact, the teeth resemble those of *Aegyptopithecus*, a much larger Fayum hominoid known from several skulls and faces, says Duke's Simons, who runs the Fayum field effort.

The chief concern about the Algerian fossils was their age, which Godinot and Mahboubi estimate to be between 46 million and 50 million years old. That estimate is based on algae found at the field site, which are similar to European algae from that time period. But the algal correlations have not yet been published and a younger age cannot be ruled out.

If Godinot's age estimate is confirmed, it would certainly add fuel to the "third-group" fire: If true anthropoids were already present 50 million years ago in Africa, then contemporaneous adapids and omomyids from North America and Europe may be irrelevant to anthropoid origins.

Ford summed up one version of the new hypothesis this way: The early primate radiation happened earlier than was previously supposed, perhaps as many as 60 million years ago. It involved three groups—omomyids, adapids, and early anthropoids—and was centered in Africa or possibly Asia. Several million years later one group, the adapids, moved north into Europe. The omomyids diversified in Asia and spread to North America. The anthropoids continued to diversify in Africa and possibly moved into Asia by about 45 million years ago.



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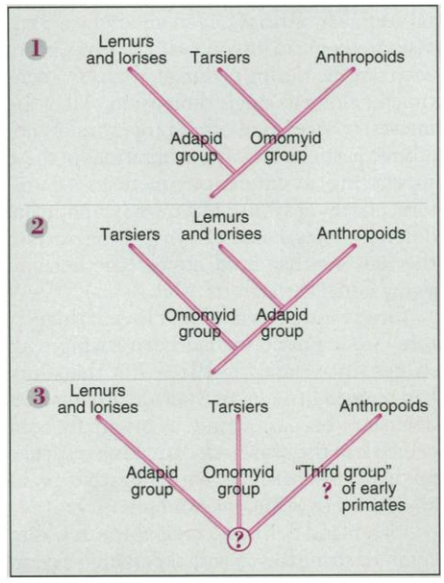
Younger cousin? *Algeripithecus minutus* is older and smaller, but its teeth resemble those of this hominoid *Aegyptopithecus*.

But this "third-group" theory is still speculative because there are few fossils from Africa and Asia during the right time period. At the workshop, Duke's Matt Cartmill noted that hypothesizing an ancestor from an unknown group of animals in a poorly sampled continent is another way to say, "We don't know." And the old hypotheses are by no means dead. For example, Gingerich of Michigan and Jens Franzen of the Senckenberg Museum in Frankfurt, Germany, believe that the "third group" is likely to be similar to adapids. And while Fred Szalay of Hunter College agrees that the missing ancestors are likely to turn up in Africa or Asia, he's convinced that they'll look like omomyids.

One reason the omomyid hypothesis will be hard to displace is that it has another bit of evidence going for it, namely the living primate, *Tarsius*. This odd little creature appears to be descended from omomyids and also is linked to anthropoids by embryological, skeletal, and molecular similarities. That presents a paradox for hardline third-group fans, who might prefer to link tarsiers to other prosimians not on the anthropoid path, such as lemurs. Duke's Simons argues that even the multiple lines of evidence aren't convincing because *Tarsius* is so specialized for its own peculiar mode of life. It is the only primate that spurns every kind of plant material as food, living entirely off insects and small vertebrates such as lizards. And since it is a nocturnal visual predator, *Tarsius* has huge eyes—each of which is bigger than its brain—to catch its prey. Thus Simons argues that some of the characteristics that link tarsiers and anthropoids, such as the flange of bone behind the eye, may be related to tarsiers' unique physiology and not their family tree.



Out on a limb. In the emerging view (bottom tree), anthropoids descended from a new third group of primitive primates, not the omomyids or adapids as previously thought.

While omomyids and adapids have dominated the discussions, other candidates for the first anthropoid have also been proposed, although at least one of these went down in flames at the Duke workshop, too. In the mid-1980s, Russell L. Ciochon of the University of Iowa claimed in papers in both *Nature* and *Science* that two relatively large, robust primates from Burma, roughly 45 million years old, represented the first known anthropoids. But the accumulation of smaller and more primitive anthropoids from the Fayum site in Egypt convinced Ciochon to change his mind. At the conference, he withdrew his claim that one of the Burmese taxa, *Pondaungia*, is an anthropoid. "I'm stepping back from that idea....I'm trying to nicely eat my words," he told a rapt audience. He thinks the other Burmese taxon, *Amphipithecus*, may still be an anthropoid but says more complete fossils are needed to interpret its evolutionary relationships.

Meanwhile, Godinot and Mahboubi's Algerian primate now appears to be the leading candidate for the first anthropoid, although whether it will hold that status remains to be seen, as the Chinese fossils are scrutinized and more specimens are unearthed from both Asia and Africa. The cantankerous crowd at the workshop did agree on one thing: At the moment, the best way to untangle this evolutionary puzzle is through fossils. Watch for more specimens—from the right places—to answer the anthropoid riddle.

–Elizabeth Culotta